



Review

Internalization of *Salmonella enterica* by tomato fruit

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ABSTRACT

Since 1990, several outbreaks of foodborne illness have been associated with the consumption of raw tomatoes. Various serovars of the bacterial pathogen, *Salmonella enterica*, were responsible for these illnesses. Fruits and vegetables are not a normal niche for mammalian pathogens. Hypotheses concerning introduction of *Salmonella* into tomatoes range from contamination in the field or greenhouse to direct or cross-contamination during harvest, handling and preparation of tomato as a raw agricultural commodity. Many different reports have shown that *Salmonella* can not only survive in tomato fruit but also proliferate from small, relatively inconsequential populations to numbers known to incite illness even in healthy individuals.

Herein, production, harvest and handling of fresh market tomatoes are evaluated in terms of how *Salmonella* might contaminate this crop. Physical principles are emphasized, whereas biological factors are included where appropriate. *Salmonella* is viewed as a bacterium that is affected by the same physical principles affecting bacteria naturally occurring in the environment surrounding tomato fruit as well as tomato plants during production, harvest and handling.

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1. Introduction

Survival of bacteria including mammalian pathogens on plants depends on microbe adaption and location on or in plant tissues (Beattie, 2002). Bacteria introduced to plant surfaces are exposed to

an array of stresses including UV (electromagnetic radiation), desiccation, temperature fluctuation, and nutrition. Protected systems such as greenhouses or high-tunnels block UV as well as moderate desiccation and temperature stresses. Weather events in open fields that limit potential stresses to microbes located on

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plants including rainfall or fogs do so only temporarily. However, in all production systems, microorganisms located in free spaces within plant tissues would be protected from environmental stresses as well as potential exposure to sanitizers after harvest. Moreover, photo-assimilates appear to be located in the water lining these free spaces and would be available as nutrition for internalized bacteria. Whether the migration of any bacterium into internal free-spaces of plants stimulates a plant cell self-defense response is unclear. Bacteria were recognized as common inhabitants of a tomato fruit's intercellular free space (Samish & Etinger-Tulczynska, 1963) well before plant host defense systems such as production of pathogenesis-related (PR) proteins was reported.

How mammalian pathogens internalize in plants under natural conditions is also not clear. Direct root uptake seems unlikely since these bacteria must compete with an array of soil-borne microorganisms for colonization sites on the root surface. Wounds on root surfaces might provide access to the internal environment of a root, but several tightly packed layers of plant cells normally exist between wounds and xylem vessels, which are essentially water-filled hollow tubes where systemic movement is possible. Moreover, research on the architecture of xylem vessels in tomato plants strongly suggested that xylem fluid moves through pit membranes before entering a petiole (van der Schoot & van Bel, 1989). Thus, it is highly questionable if direct and continuous water columns exist between the root of a tomato plant and pulp of its fruit. In contrast with morphological obstacles to direct root uptake, external water could transport otherwise surface resident or casual microbes into the apoplastic free space of a fruit. Infiltration of apertures on plant surfaces by external water could be caused by hydrostatic pressure on plant surfaces, or internal vacuums caused by a cooling of gasses within plant tissues.

Apertures, including stomata, hydathodes, lenticels, are a necessary feature of large, bulky storage organs (e.g., fruit, tubers, etc.). To carry out normal respiration, cells within these storage organs require access to oxygen. Surface apertures that enable gas exchange are connected to the intercellular free-space network of the storage organ. External water can flood into these apertures due to hydrostatic pressure, a physical force directed on fruit surfaces during contact with water including fruit dumped into water, fruit struck by rainfall, overhead irrigation or wash-water or fruit submerged under water. External water can also be drawn into surface apertures due to internal vacuums that develop when gasses within a fruit's apoplastic free space cool leading to pressure gradients between the cuticle surface and internal storage tissues (Corey & Tan, 1990). Infiltration is likely when aqueous films cover a cooling fruit's surfaces such as those surrounding a submerged tomato fruit. Alternatively, if water uptake by a plant's root system exceeds transpiration, free water may appear within the petiole apoplast and extend to and out of hydathodes of tomato leaves (Johnson, 1945). This water column provides a liquid pathway for surface microbes to enter the internal apoplast of those leaves. The extent of such liquid pathways in fruit still attached to a plant is unclear. Fruit are known to crack in response to excessive water uptake by roots, which suggests that high water potentials within the apoplast cause cells to absorb water and swell at a time when the outer fruit surface has lost elasticity.

1.1. *Salmonella*

Salmonella is a common cause of foodborne bacterial illness in the US, ranking second behind norovirus in terms of number of cases (Scallan et al., 2011). The non-host adapted *Salmonella* serovars causing salmonellosis outbreaks are inhabitants of the intestinal tract of a wide range of animals (Abulreesh, 2012; Todar,

2005). The bacterium is infectious at a range of populations with a minimum infectious dose for certain members of the general population of 15–20 cells (FDA, 2003) up to log 9.0 cfu for 50% of a population of healthy individuals (Todar, 2005). Predominant sources of *Salmonella* leading to outbreaks of human gastroenteritis appear to be animal-originated foods, such as poultry meat, eggs, and dairy products (Abulreesh, 2012). However, outbreaks of salmonellosis have been traced back to consumption of raw fruits and vegetables (FDA, 2009). For example, consumption of raw tomatoes was responsible for an outbreak of salmonellosis in 1990. Since that event, up to 15 additional outbreaks have been traced back to tomato fruit (Bartz, 2009) (Table 1).

However, except for one report (Wells & Butterfield, 1997), the detection of *Salmonella* in tomato fruit in the field or marketing chain has been rare. Gorny (2006) noted that *Salmonella* was not detected among 2924 samples of tomatoes that had been analyzed by FDA (two surveys) and USDA (one survey) for pathogens. Sapers & Doyle (2009) concluded that contamination of most fresh produce, and not just tomatoes, by enteric pathogens was too low to detect by “broadly focused surveys.”

2. Outbreaks of salmonellosis traced back to tomatoes

Serotypes recovered from patients have varied among outbreaks (Table 1). Traceback investigations concluded that fruit were contaminated in the field primarily because outbreaks were multistate. Suggested sources ranged from animals in nearby pastures or wetlands to water used for irrigation or pesticide applications. One outbreak involved several serotypes, whereas each of the rest was attributed to a serotype that had a unique pulsed-field gel electrophoresis (PFGE) fingerprint. Environmental investigations failed to detect the implicated serotype(s) in fields or packinghouses during or immediately after outbreaks. A relatively short harvest/marketing cycle was a suggested reason for this failure.

Variation among serotypes of *Salmonella enterica* for survival and/or proliferation in fruit and leaf tissues of tomato plants has been reported but none tested have shown a marked ability to colonize (Guo, Chen, Brackett, & Beuchat, 2002; Guo, Van Iersel, Chen, Brackett, & Beuchat, 2002; Marvasi et al. 2013; Shi, Namvar,

Table 1
Summary for *Salmonella* outbreaks associated with the consumption of raw tomatoes from 1990 to 2006 in the United States.

Year	Tomato type	Agent	Source	Number of ill	Reference
1990	Round	S. Javiana	SC	176	Hedberg et al., 1999
1993	Round	S. Montevideo	SC	100	Hedberg et al., 1999
1998	Round	S. Baildon	FL	86	Cummings et al., 2001
2000	Round	S. Thompson	FL or GA	43	–
2002	Round	S. Newport	VA	512	Kretsinger, 2003
2002	Grape	S. Newport	FL	12	–
2002	Roma	S. Javiana	FL	141	CDC, 2002; Srikantiah et al., 2005
2004	Roma	Multiple ^a	FL, GA or SC	429	CDC, 2005
2004	Roma	S. Braenderup	FL	125	CDC, 2005
2005	Round	S. Newport	VA	71	Greene et al., 2008
2005	Round	S. Braenderup	FL	76	–
2006	Round	S. Newport	VA ^b	115	CDC, 2007
2006	Round	S. Typhimurium	OH	190	CDC, 2007

^a Serotypes reported include (with# reported cases): S. Javiana (383), S. Typhimurium (27), S. Anatum (5), S. Thompson (4), S. Muenchen (4), and Group D untypable (6).

^b Fruit source was not determined but PFGE pattern was identical to that collected in 2005 outbreak associated with tomatoes from Delmarva Peninsula.

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